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ORIGINAL PAPER

Halomarinibacterium sedimenti gen. nov., sp. nov., a carotenoid pigment-producing bacterium isolated from marine sediment

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Abstract

A Gram-negative, strictly aerobic, non-motile, rod-shaped bacterial strain CAU 1614^T was isolated from a marine sediment sample collected in the Republic of Korea. Optimal growth of strain CAU 1614^T proceeded at 30 °C, pH 7.0, and 2% (w/v) NaCl. 16S rRNA gene similarity was lower than 94.5% with genera *Aureisphaera*, *Marinirhabdus*, *Aureitalea*, *Gilvibacter*, *Ulvibacter*, and *Jejudonia*. The highest similarity was with *Aureisphaera galaxeae* 04OKA003-7^T (94.5%). The major cellular fatty acids were iso-$C_{15:0}$, iso-$C_{16:0}$, iso-$C_{15:1}$ G, iso-$C_{16:0}$ 3-OH, and iso-$C_{17:0}$ 3-OH and the predominant menaquinone was MK-6. The polar lipids were phosphatidylethanolamine, phosphoglycolipid, an unidentified lipid, two unidentified aminolipids, and an unidentified glycolipid. The draft genome of strain CAU 1614^T was 3.9 Mb and DNA G+C content was 36.0 mol%. On the basis of the phenotypic, chemotaxonomic, and genomic data, strain CAU 1614^T presents a novel genus in the family *Flavobacteriaceae*, for which the name *Halomarinibacterium sedimenti* gen. nov., sp. nov. is proposed. The type strain is CAU 1614^T (= KCTC 82457^T = MCCC 1K06083^T).

Keywords *Halomarinibacterium sedimenti* · *Flavobacteriaceae* · Marine sediment · Genome · 16S rRNA · Novel genus

Introduction

The family *Flavobacteriaceae* is a member of the order *Flavobacteriales* initially proposed by Reichenbach (1992) and emendated by Bernardet et al. (1996, 2002) and, more recently, García-López et al. (2019) based on genome information. According to the List of Prokaryotic names with Standing in Nomenclature (LPSN), *Flavobacteriaceae* comprises 151 validly published genera (https://lpsn.dsmz.de/family/flavobacteriaceae). *Flavobacteriaceae* is characterized as Gram-negative rod-shaped cells and MK-6 as the predominant respiratory quinone (Bernardet et al. 2002).

Strain CAU 1614^T was isolated from a marine sediment sample during an investigation of the marine novel bacterial diversity in the Republic of Korea. The purpose of this study was to examine its taxonomic position and characterization via phenotypic, chemotaxonomic, and genome-based approaches.

Materials and methods

Bacterial strain and culture conditions

Strain CAU 1614^T was isolated from a marine sediment sample collected from Ayajin, Gangwon-do (38° 16′ 32.0″ N 128° 33′ 12.0″ E), the Republic of Korea. The sample was serially diluted with sterilized 0.85% NaCl solution several times and 100 µl of the diluent was spread onto marine agar 2216 (MA; BD Difco, Sparks, MD, USA) plate. After 7 days of incubation under aerobic conditions at 30 °C, yellow colonies of strain CAU 1614^T were harvested and purified by re-streaking onto fresh MA plates more than three times. The purified culture of strain CAU 1614^T was harvested and preserved in marine broth 2216 (MB) supplemented with

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25% (v/v) glycerol at – 80 °C. The type strains of the species in closely related genera *Aureisphaera*, *Marinirhabdus*, *Aureitalea*, *Gilvibacter*, *Ulvibacter*, and *Jejudonia* were used as reference strains. *Aureisphaera galaxeae* KCTC 32993^T, *Aureisphaera salina* KCTC 42975^T, *Marinirhabdus citrea* KCCM 43216^T, *Aureitalea marina* KCTC 23434^T, *Gilvibacter sediminis* NBRC 101626^T, *Ulvibacter antarcticus* DSM 23424^T, and *Jejudonia soesokkakensis* KCTC 32325^T were obtained from the Korean Collection for Type Cultures (KCTC; Jeollabuk-do, Korea), the Korean Culture Center of Microorganisms (KCCM; Seoul, Korea), the National Institute of Technology and Evaluation (NITE) Biological Resource Center (NBRC; Tokyo, Japan), and the Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH (DSMZ; Braunschweig, Germany).

Phylogenetic analysis

Genomic DNA from strain CAU 1614^T was prepared using a bacterial genomic DNA extraction kit (iNtRON, Seongnam, Korea), and 16S rRNA gene fragments were amplified via polymerase chain reaction (PCR) (Nam et al. 2004). The sequence was determined using a BigDye Terminator Cycle Sequencing Kit and a 3730 Automated DNA Sequencer (Applied Biosystems, Foster City, CA, USA). The 16S rRNA gene sequence similarities between strain CAU 1614^T and closely related strains were determined by referencing the NCBI GenBank database (https://www.ncbi.nlm.nih.gov/genbank/). Multiple alignments and phylogenetic tree construction with neighbor-joining (Saitou and Nei 1987), maximum-parsimony (Fitch 1971), and maximum-likelihood (Felsenstein 1981) methods were performed using MEGA7 software. Bootstrap analysis resampling with 1000 replicates was conducted to estimate the branch support (Felsenstein 1985).

Whole-genome sequence analysis

The whole genome of strain CAU 1614^T was extracted using a TruSeq DNA PCR-Free kit (Illumina, San Diego, CA, USA). The sequence data were obtained using an Illumina Hiseq sequencer (Illumina). Assembling the sequences was performed via SPAdes version 3.13.0 (http://cab.spbu.ru/software/spades) and *K*-mer analysis was performed via Jellyfish (version 2.2.3) (http://www.genome.umd.edu/jellyfish.html) and GenomeScope (http://qb.cshl.edu/genomescope). Any contamination and the authenticity of the 16S rRNA gene sequence with PCR amplification were determined using the Basic Local Alignment Search Tool (BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi). The digital DNA–DNA hybridization (dDDH), average nucleotide identity (ANI), and average amino acid identity (AAI) values between strain CAU 1614^T and the reference strains with genome data on the National Center for Biotechnology Information (NCBI) database were calculated using the Genome-to-Genome Distance Calculator (GGDC; http://ggdc.dsmz.de/ggdc.php), OrthoANI program (http://www.ezbiocloud.net/sw/oat), and AAI calculator (http://enve-omics.ce.gatech.edu/aai/), respectively. DNA–DNA hybridization (DDH) between strain CAU 1614^T and most closely related strain without genomic data on NCBI was performed as described previously (Ezaki et al. 1989). The G+C content was calculated based on the genome sequence of strain CAU 1614^T. Proteome comparison was verified using the PATRIC webserver (www.patricbrc.org). The whole-genome sequence of strain CAU 1614^T was annotated through the Rapid Annotation Using Subsystem Technology (RAST) webserver (http://rast.nmpdr.org/rast.cgi). Various secondary metabolite-related biosynthetic gene clusters (BGCs) were identified via antiSMASH version 6.0.1 (https://antismash.secondarymetabolites.org). The phylogenetic tree based on core genes constructed using UBCG version 3.0 (https://www.ezbiocloud.net/tools/ubcg).

Physiological, morphological, and biochemical analysis

The morphological characteristics of colonies of strain CAU 1614^T, including color, texture, shape, and size, were examined after 3 days on MA at 30 °C. Morphological analysis of cells was conducted under a DM 1000 light microscope (Leica, Wetzlar, Germany). The presence of flagella was determined via a JEM 1010 transmission electron microscopy (JEOL, Tokyo, Japan). The gliding motility was examined using the hanging-drop method described by Bowman (2000). Gram staining was performed with a Gram staining kit (bioMérieux, Craponne, France). CAU 1614^T was grown in MB at various temperatures (4, 10, 15, 20, 25, 30, 37, and 45 °C) and pH values (4.5–11.5 at 0.5 pH unit intervals and adjusted with 1 M HCl or 1 M NaOH) to determine the optimal growth conditions. Likewise, cells were grown in NaCl-free MB formula broth at various concentrations of NaCl (0–15% (w/v); at 1% (w/v) intervals) to establish the optimal NaCl concentration. The turbidity of the broth was measured after 72 h. Growth under anaerobic conditions was examined in a BACTRON anaerobic chamber (Sheldon Manufacturing, Cornelius, USA). MA, glucose yeast extract agar (GYE), nutrient agar (NA; Difco), brain heart infusion agar (BHI; Difco), tryptic soy agar (TSA; Difco), and Luria agar (LA; Difco) were used to explore its growth on a variety of media. Oxidase and catalase activity were tested with 1% (w/v) tetramethyl-*p*-phenylenediamine and 3% (v/v) hydrogen peroxide solution, respectively (Cappuccino and Sherman 2010). Various enzyme activity and biochemical tests were performed using API 50CH, API 20NE, and API ZYM kits (bioMérieux). Hydrolyses of casein and starch

were examined according to the method of Smibert and Krieg (1994).

Chemotaxonomic characterization

Polar lipids were extracted and separated using two-dimensional thin-layer chromatography with a silica gel plate (60 F254; Merk, NJ, Kenilworth, USA) using the protocol according to Minnikin et al. (1984) plates were sprayed with 10% ethanolic molybdophosphoric acid for total lipids, ninhydrin for aminolipids, α-naphthol reagent for glycolipids, molybdenum blue for phospholipids, and Dragendorff's reagent for choline, respectively (Kim et al. 2015). Respiratory quinones were extracted and analyzed as described previously (Sasser 2006). Cellular fatty acids were extracted according to the standard Microbial Identification System (MIDI) protocol and separated by 6890 N gas chromatography (Agilent, Santa Clara, CA, USA). The peaks were analyzed using microbial identification software package MMORE library (MIDI database TSBA6).

Results and discussion

Phenotypic and biochemical characteristics

Strain CAU 1614^T was a Gram-negative rod-shaped, aerobic, non-motile, and non-flagellated (Fig. S1). Colonies of strain CAU 1614^T were yellow, circular, and opaque with a smooth texture after incubation at 30 °C for 3 days. The growth of strain CAU 1614^T occurred in a temperature range of 20 to 37 °C, a pH range of pH 6.0–8.0, and an NaCl concentration range of 0–2% (w/v) with optima of 30 °C, pH 7.0, and 2%w/v NaCl, respectively. Strain CAU 1614^T grew well on an MA plate but not on NA, GYE, TSA, BHI, or LA plates. The detailed morphological, physiological, and biochemical characteristics of strain CAU 1614^T and related strains of the family *Flavobacteriaceae* are reported in Table 1. Strain CAU 1614^T was oxidase- and catalase-positive but cannot hydrolyze casein, starch, or urea. Esculin and potassium 5-ketogluconate were utilized as carbon sources. The narrow NaCl tolerance range (0–2.0% (w/v)) distinguished strain CAU 1614^T from the genera *Aureisphaera* (0–5.5% (w/v)), *Marinirhabdus* (0.5–6.0% (w/v)), *Aureitalea* (0–4.5% (w/v)), *Gilvibacter* (0.5–6.0% (w/v)), *Ulvibacter* (1–3.0% (w/v)), and *Jejudonia* (1.0–5.0% (w/v)). Moreover, strain CAU 1614^T differed from the most closely related strain *Aureisphaera galaxeae* 04OKA003-7^T by being positive for esterase (C4), esterase lipase (C8), cysteine arylamidase, trypsin, and α-chymotrypsin.

Phylogenetic and genome characterization

The 16S rRNA gene sequence of strain CAU 1614^T (1450 bp) was obtained and compared with closely related species from the NCBI database (access March 2022). Strain

Table 1 Different characteristics of strain CAU 1614^T and closely related type strains of the family *Flavobacteriaceae*

Characteristic	1	2	3	4	5	6	7	8
Temperature range (°C)	20–37	20–30	20–37	17–38	15–30	15–37	3–25	10–30
NaCl range (%, w/v)	0–2.0	0–5.5	0.5–6.0	0–4.5	0.5–6.0	0–6.0	1.0–3.0	1.0–5.0
Hydrolysis								
Urease	–	+	+	+	–	–	–	–
Carbon utilization								
D-Maltose	–	+	+	+	+	–	–	+
D-Cellobiose	–	+	+	–	–	–	–	–
Enzyme activities								
Alkaline phosphate	+	+	+	+	+	–	+	+
Leucine arylamidase	+	+	+	+	+	–	+	+
Cystine arylamidase	+	–	–	+	+	–	–	+–
Valine arylamidase	+	+	+	+	+	–	+	+
Typsin	+	–	–	+	+	–	–	–
Acid phosphatase	+	+	+	+	+	–	+	–
Naphtol-AS-BI-phosphohydrolase	+	+	+	+	+	–	+	–
Major polar lipid	PE, PGL	PE	PE	PE	DPG, PG	–	–	PE
DNA G+C content (mol%)	36.0	41.0	40.8	43.1	48.1	39.0	37.0	39.9

Strain: 1, CAU 1614^T; 2, *Aureisphaera galaxeae* KCTC 32993^T (Yoon et al. 2015); 3, *Aureisphaera salina* KCTC 42975^T (Yoon et al. 2016); 4, *Marinirhabdus citrea* KCCM 43216^T (Yang et al. 2018); 5, *Aureitalea marina* KCTC 23434^T (Park et al. 2012); 6, *Gilvibacter sediminis* NBRC 101626^T (Khan et al. 2007); 7, *Ulvibacter antarcticus* DSM 23424^T (Choi et al. 2007); 8, *Jejudonia soesokkakensis* KCTC 32325^T (Park et al. 2013). +, Positive; –, negative. PE, phosphatidylethanolamine; DPG, diphosphatidylglycerol; PG, phosphatidylglycerol; PGL, phosphoglycolipid

CAU 1614^T shows the closest similarity to *Aureisphaera galaxeae* 04OKA003-7^T (94.5%), followed by *Aureisphaera salina* A6D-50^T (94.3%) and *Marinirhabdus citrea* MEBiC09412^T (93.5%), all of which belong to the family *Flavobacteriaceae*. The phylogenetic tree constructed based on the 16S rRNA gene showed the clusters of strain CAU 1614^T and related strains in *Flavobacteriaceae* (Fig. 1). The phylogenetic tree between it and the members of *Flavobacteriaceae* constructed based on core genes indicates that it is a novel strain from a new genus in *Flavobacteriaceae* (Fig. 2). The results of the phylogenetic analysis of the 16S rRNA gene show that strain CAU 1614^T should be distinguished as a novel taxon in *Flavobacteriaceae*.

The whole genome of strain CAU 1614^T (3.9 Mb in size) contained 15 contigs with an average length of 197,169 bp. The N50 value was 580,342 bp and the *K*-mer coverage was 175x. Strain CAU 1614^T included 2679 protein-coding genes, 3 rRNAs (5S, 16S, and 23S), and 35 tRNAs in the

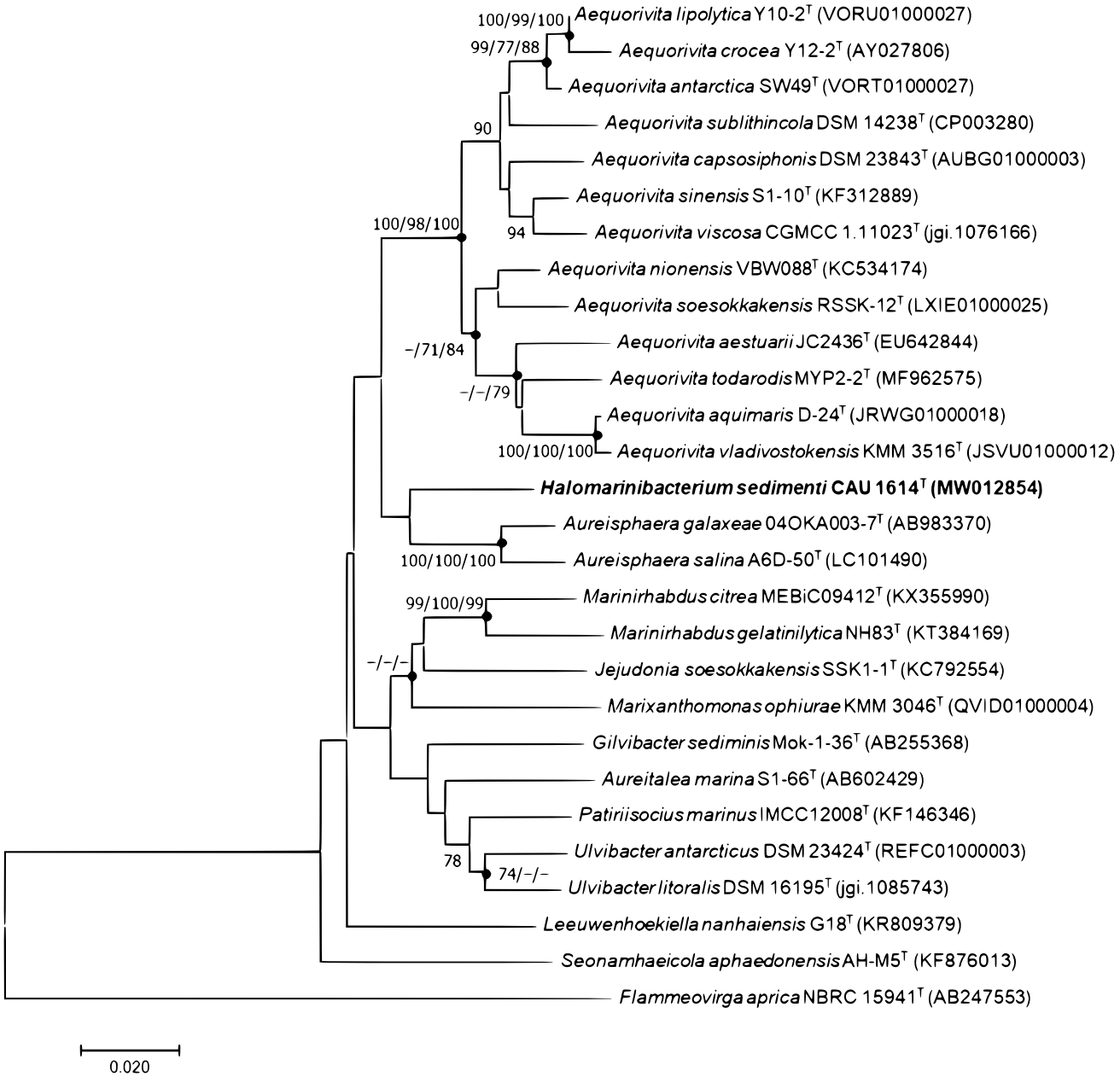

Fig. 1 The neighbor-joining tree based on nearly complete 16S rRNA gene sequence of strain CAU 1614^T and closely related strains showing the relationship between strains. Bootstrap value > 70% based on 1000 resampling to neighbor-joining, maximum-likelihood and maximum-parsimony analyses (NJ/ML/MP) given. Bar, 0.02 substitutions per position. *Flammeovirga aprica* NBRC 15941^T (AB247553) was used as outgroup species

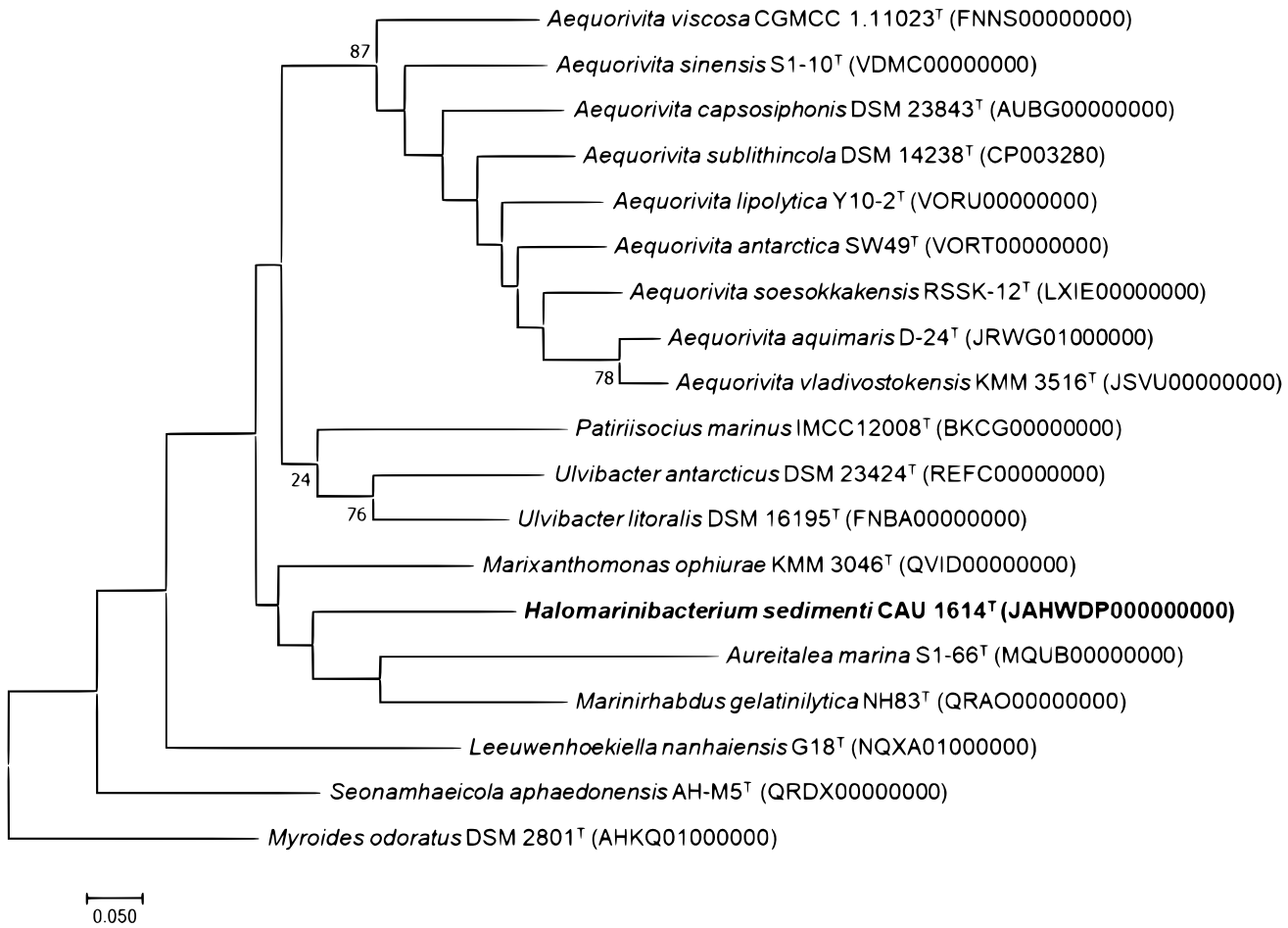

Fig. 2 The phylogenetic tree based on core genes of strain CAU 1614^T and closely related strains constructed using UBCG program. Bootstrap value > 70% are shown. *Myroides odoratus* DSM 2801^T (AHKQ01000000) was used as outgroup species

draft genome. The DNA G+C content calculated based on the whole genome was 36.0 mol%, which is in the range of 30–42% reported for the family *Flavobacteriaceae*. The genome of strain CAU 1614^T was not contaminated (the 16S rRNA gene sequence similarity with the PCR amplification result was 99.9%). The DDH value of strain CAU 1614^T between *Aureisphaera galaxeae* 04OKA003-7^T was 43.9%. Ortho ANI, dDDH, and AAI values between strain CAU 1614^T and *Aureitalea marina* S1-66^T were 68.4%, 19.7%, and 65.4%, respectively, while those between strain CAU 1614^T and *Ulvibacter antarcticu* DSM 23424^T were 70.9%, 18.6%, and 67.92%, respectively (Table S1). All of the values were below the thresholds proposed by Meier-Kolthoff et al. (2013) and Lee et al. (2016) for describing novel species. The proteome comparison results show that strain CAU 1614^T and related strains share proteins with 10–90% similarity (Fig. S2). The annotated functional genes in the genome of strain CAU 1614^T were 917 (Fig. S3). The most (> 100) were categorized as cofactors, vitamins, prosthetic groups, pigments (117 genes), protein metabolism (138 genes), amino acids and derivatives (181 genes), and carbohydrates (106 genes). It contained one secondary metabolite gene cluster verified as a terpene and showed 28% similarity with the carotenoid biosynthetic gene cluster in *Algoriphagus* sp. KK10202C (Table S2). The carotenoid biosynthesis is one of the characteristics of the family *Flavobacteriaceae* for yellow pigment (Bernadet et al. 2002) and strain CAU 1614^T contained carotenoid biosynthetic gene cluster and produce yellow pigment. The genome of strain CAU 1614^T was deposited in the GenBank/EMBL/DDBJ under accession number JAHWDP000000000.

Chemotaxonomic characterization

The major fatty acids (> 10%) identified in strain CAU 1614^T were iso-$C_{15:0}$ (19.5%), iso-$C_{16:0}$ (11.2%), iso-$C_{15:1}$ G (11.0%), iso-$C_{16:0}$ 3-OH (17.5%), and iso-$C_{17:0}$ 3-OH (11.8%). The fatty acid profiles of strain CAU 1614^T and related type strains in the family *Flavobacteriaceae* provided in Table S3 show that their major fatty acid compositions

are mostly similar. However, iso-$C_{17:0}$ 3-OH was observed in strain CAU 1614^T and all of the reference strains except for *U. antarcticus* DSM 23424^T, which only has $C_{18:1}$ *ω7c* 11-methyl (10.1%) and summed feature 8 ($C_{18:1}$ *ω6c* and/or $C_{18:1}$ *ω7c*) (72.5%). The polar lipids detected in strain CAU 1614^T were phosphatidylethanolamine, phosphoglycolipid, unidentified lipid, two unidentified aminolipids, and unidentified glycolipid (Fig. S4). The results show that although strain CAU 1614^T and the reference strains had the same major polar lipid, strain CAU 1614^T differed from other members in the family *Flavobacteriaceae* due to the presence of phosphoglycolipid (Table 1). The predominant quinone in strain CAU 1614^T was menaquinone 6 (MK-6).

Taxonomic conclusion

The results of the phylogenetic analysis based on genome data evidence show the genera and phenotype clusters for strain CAU 1614^T, and the chemotaxonomic data support these results. Therefore, we determined that strain CAU 1614^T is a novel species in a novel genus, which we have named *Halomarinibacterium sedimenti* gen. nov. sp. nov.

Description of Halomarinibacterium gen. nov.

Halomarinibacterium (Ha.lo.ma.ri.ni.bac.te'ri.um. Gr. masc. n. *hals*, *-halos*, salt; L. adj. *marinus*, of the sea, marine; N.L. neut. n. *bacterium*, a small rod; N.L. neut. n. *Halomarinibacterium*, a halophilic marine rod.) (Table 2).

Cells are Gram-negative, non-motile, rod-shaped, and strictly aerobic, positive for oxidase and catalase. The only menaquinone is MK-6 and the predominant fatty acids are iso-$C_{15:0}$, iso-$C_{16:0}$, iso-$C_{15:1}$ G, iso-$C_{16:0}$ 3-OH, and iso-$C_{17:0}$ 3-OH. The major polar lipids are a phosphoglycolipid and phosphatidylethanolamine.

Description of Halomarinibacterium sedimenti sp. nov.

Halomarinibacterium sedimenti sp. nov. (sed.i.men'ti. L. gen. n. *sedimenti*, sediment, from which the type strain was isolated).

Cells are Gram-negative, strictly aerobic, non-motile, and rod-shaped, approximately 0.2–0.3 μm in width and 3.0–2.0 μm in length. Colonies are yellow-colored, circular, opaque with a smooth texture, and 0.5–0.8 mm in diameter on MA after 3 days incubation at 30 °C. Optimal growth conditions are 30 °C, pH 7.0, and 2%w/v NaCl. Catalase and oxidase are present. Casein, starch, and urea hydrolysis are not present. Esculin and potassium 5-ketogluconate are used as carbon sources. Enzyme activity is positive for esterase (C4), esterase lipase (C8), alkaline phosphatase, cysteine arylamidase, leucine arylamidase, valine arylamidase, trypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α-chymotrypsin, α-galactosidase, α-glucosidase, and β-glucosidase. The major polar lipids are a phosphoglycolipid and phosphatidylethanolamine. iso-$C_{15:0}$, iso-$C_{16:0}$, iso-$C_{15:1}$ G, iso-$C_{16:0}$ 3-OH, and iso-$C_{17:0}$ 3-OH are major fatty acids.

Table 2 Different characteristics between genus *Halomarinibacterium* and related genera in the family *Flavobacteriaceae*

Characteristic	1	2	3	4	5	6	7
Cell form	Rod	Rod, coccus	Rod	Rod	Rod	Rod	Rod
Colony color	Yellow	Pale yellow, yellow	Yellow	Yellow	Yellow	Yellow	Yellow
Motility	–	–	–	+	–	–	–
Growth temperature	20–37	20–37	4–38	15–30	15–37	3–37	10–30
Major fatty acid	iso-$C_{15:0}$, iso-$C_{16:0}$, iso-$C_{15:1}$ G, iso-$C_{16:0}$ 3-OH, iso-$C_{17:0}$ 3-OH	iso-$C_{15:0}$, iso-$C_{17:0}$ 3-OH	iso-$C_{15:0}$, iso-$C_{17:0}$ 3-OH	iso-$C_{15:0}$, iso-$C_{15:1}$ G, iso-$C_{17:0}$ 3-OH	iso-$C_{15:0}$, iso-$C_{15:1}$ G, iso-$C_{16:0}$ 3-OH, iso-$C_{17:0}$ 3-OH	iso-$C_{15:0}$, iso-$C_{15:1}$ G	iso-$C_{15:0}$, iso-$C_{16:0}$, anteiso-$C_{15:0}$
Major polar lipid	PE, PGL	PE	PE	DPG, PG	–	PE	PE
DNA G+C content (mol%)	36.0	40.8–41	41–43.1	48.1	43	36.7–38.1	39.9

Genus: 1, *Halomarinibacterium*; 2, *Aureisphaera*; 3, *Marinirhabdus*; 4, *Aureitalea*; 5, *Gilvibacter*; 6, *Ulvibacter*; 7, *Jejudonia*

+, Positive; –, negative. PE, phosphatidylethanolamine; DPG, diphosphatidylglycerol; PG, phosphatidylglycerol; PGL, phosphoglycolipid

The type strain CAU 1614^T (= KCTC 82457^T = MCCC 1K06083^T) was isolated from a marine sediment sample from Ayajin, Gangwon-do, Republic of Korea.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-022-03140-0.

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Author's contribution Conceived and designed the experiments: W.K., Conducted the experiments: J.J., V.W., Y.L., Analyzed the data: J.-H.K., A.S., K.K., Contributed reagents, materials, and analysis tools: W. K., Wrote the paper: J.J., K.K., W.K.

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Data availability The 16S rRNA sequence and whole-genome sequence of strain CAU 1614^T were obtain to the GenBank/EMBL/DDBJ as MW012854 and JAHWDP000000000, respectively.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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